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STUDIES OF '*PORTUNUS GLADIATOR* COMPLEX' AND RELATED SPECIES OF *PORTUNUS* (CRUSTACEA: DECAPODA).

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ABSTRACT

Confusion over *Portunus gladiator* Fabricius *P. gladiator*: Stephenson and Campbell, and *P. pseudoargentatus* Stephenson has been resolved. The species normally regarded as *P. gladiator* Fabricius becomes *P. haanii* (Stimpson); the species first named *Cancer gladiator* by Fabricius is synonymised with *P. sanguinolentus* (Herbst) and a neotype of *Cancer gladiator* has been deposited in the Queensland Museum. *P. pseudoargentatus* is a synonym of *P. haanii*, and *P. gladiator*: Stephenson and Campbell becomes *P. australiensis* sp. nov.

In 1959 Stephenson and Campbell identified two Australian portunids as *P. gladiator* Fabricius and gave a reasonably full description. In 1962 Crosnier, in reporting upon Madagascar portunids noted three main differences between material he identified as *P. gladiator* Fabricius and the descriptions of Stephenson and Campbell. While noting that these may have been due to size differences, he thought that two different species were involved. This was confirmed by Stephenson and Rees (1967a) who decided that a decision upon which of the two forms should be referred to Fabricius's species should await critical examination of Fabricius's material.

Through the kindness of Dr T. Wolff of the University Zoologiske Museum, Copenhagen, one of the original specimens upon which *P. gladiator* Fabricius, 1798 was based has been available for study, and photographs of a second specimen have been provided. It thus became clear that Crosnier's material belonged to Fabricius's species of 1798.

Meanwhile in 1961 Stephenson described a third species of the present 'complex'—*P. pseudoargentatus*. Crosnier (1962) in recording two Japanese specimens of this species in European museums, previously identified as *P. gladiator*, noted the probability of past confusions between *P. gladiator* and *P. pseudoargentatus*. It was clearly desirable to examine as many relevant specimens as possible, particularly because it became evident

that *P. gladiator* Fabricius varied in features which had been used in specific diagnoses. This necessitated biometric studies and these revealed that *P. pseudoargentatus* was a synonym of *P. gladiator* Fabricius, 1798.

A final point of confusion arises from the fact that Fabricius appears to have used the epithet *gladiator* on two occasions to refer to different species. The first use is in Fabricius (1793, p. 449) with reference to *Cancer gladiator*, and refers to specimens collected by Captain Cook in Australian waters—the details are '. . . in Nova Hollandia Mus. Dom. Banks'. We now have a considerable knowledge of the Australian portunid fauna (see for example Stephenson, 1972), and there have been only two recordings which could have been conspecific with *P. gladiator* Fabricius, 1798 in the last century. The first was by Haswell (1882) from Queensland waters. The specimens are no longer available and there is a possibility from the very general nature of Haswell's description that the material was misidentified. The second records were Stephenson's (1961) as *P. pseudoargentatus*. It would be unexpected for Captain Cook to have obtained, in his somewhat desultory collecting of portunids, a species which now appears to be anything but widespread in Australian waters.

Captain Cook's specimens are not available, and a direct check of their identity can not be made. The only relevant comments upon the specimens are by Latreille (1825, p. 190) who synonymises them with *P. sanguinolentus* (Herbst, 1783). While it appears that Latreille may not have examined the material, we do know that *P. sanguinolentus* is common on sandy bottoms in the moderately shallow waters off the Queensland coast, and might well have been obtained by H.M.S. 'Endeavour'. Since some finality is required, we have decided to accept Latreille's synonymisation. As a result *P. gladiator* Fabricius, 1798 becomes a junior homonym of *P. gladiator* (Fabricius, 1793). We have selected a specimen of *P. sanguinolentus* (Herbst, 1783) as a neotype of *P. gladiator* (Fabricius, 1793), (Male, L = 65·8 mm, B = 149·7 mm, QM W3683, 6 miles N. of Skirmish Pt, S. end Bribie I., 4–6 fm, 17.v.1972) thereby eliminating this epithet. While this is to be regretted it appears to be the only course which avoids distortion of such facts as are known.

The full synonymy of *P. gladiator* Fabricius, 1798 is given later and from this it is evident that the first acceptable name is *Amphitrite haanii* Stimpson, 1858, based upon one of de Haan's specimens of *Portunus* (*Amphitrite*) *gladiator*. Dr L. B. Holthius has kindly informed us that this specimen is existent in the Rjksmuseum, Leiden, and clearly this becomes the holotype.

Material for the present study has been borrowed from the institutions and individuals listed below, and we are deeply grateful to them: Australian Museum, (A.M.) per Dr D. J. G. Griffin; British Museum, (B.M.) per Dr R. W. Ingle; Office de la Recherche Scientifique et Technique Outre-Mer, Madagascar, per Dr A. Crosnier; Paris Museum, (P.M.) per Mme Danièle Guinot; Queensland Museum (Q.M.) per Mr B. M. Campbell; Strasbourg Museum, per Dr F. Gouin; United States National Museum, (U.S.N.M.) per Dr R. B. Manning; Univ. Zöologische Museum, Copenhagen, per Dr T. Wolff; Western Australian Museum, (W.A.M.) per Dr R. W. George. Appendix 1 lists details of all specimens within the 'complex' which were examined, while Appendix 2 lists borrowed material which had been identified as *P. gladiator* by various other workers, but which lies outside the 'complex'.

The first objective in the work was to establish whether or not '*P. gladiator* Fabricius' and *P. pseudoargentatus* Stephenson were distinct, and is detailed in the next section. Following this the synonymy of '*P. gladiator* Fabricius' is detailed and discussed, and two species in the complex are then described—these are *Portunus haanii* (Stimpson) (= *P. gladiator* Fabricius, 1798) and *P. australiensis* (= *P. gladiator*: Stephenson and Campbell, 1959).

RELATIONSHIPS BETWEEN *P. HAANII* (STIMPSON) AND *P. PSEUDOARGENTATUS* STEPHENSON

The differences between *P. gladiator*: Stephenson and Campbell and the material studied in this section are sufficiently obvious to permit distinctions by means of the normal types of specific descriptions. This did not apply to the specimens in various collections which had previously been identified as *P. gladiator* Fabricius and as *P. pseudoargentatus* Stephenson. Stephenson and Rees (1967a, p. 25) summarised the differences between the two 'species' and stated for *P. pseudoargentatus*: 'b. Form of male abdomen. The ultimate segment relatively long and without concave lateral borders, penultimate segment not swollen in distal third. c. Relatively narrower fifth merus. In *P. pseudoargentatus* breadth is about 0·75 times length in *P. gladiator* about 0·9 times.'

Examination of the present collections showed that these and other features appeared to vary with specimen size and biometric studies were undertaken in all attributes which were readily quantified. The remaining possible differences are treated in a more classical way.

(A) Biometrical Studies

The following were measured:

(1) Lengths and breadths of carapaces, using dial calipers, with results given to nearest 0·5 mm. Length was from the tips of the median frontal teeth to the mid-point of the posterior edge of the carapace. Breadth was between the tips of the last anterolateral teeth. In cases where these tips were damaged, an estimate was made to the nearest 1 mm of probable breadth before damage. From the above data length/breadth (l./b.) ratios of carapaces were derived. Because damage affected breadth, carapace lengths were used to determine whether ratios were size-dependent.

(2) Lengths and breadths of the merus of the fifth legs were measured in arbitrary units (gradations of eyepiece micrometer). Length/breadth ratios gave values approximating to 1·00 and are accurate to about 0·02.

(3) The relative concavity of penultimate segment of the male abdomen was measured as the difference between the maximum breadth of this segment (which is usually about $\frac{2}{3}$ of the length from the distal border) and the minimal breadth (about $\frac{1}{3}$ this length), divided by the minimal breadth. These values range from ca. 0·4 to zero and are accurate to about $\pm$ 0·005.

(4) Lengths of the penultimate segment were measured in the mid line, and the ratio length/maximum breadth was used as a measure of overall shape. Values approximate to unity and are accurate to about 0·02.
(5) In a similar way the length/breadth ratio of the ultimate segment was derived again to about 0·02.
(6) From the above data the ratio of the lengths of ultimate to length of penultimate segments were obtained, with accuracy again ca. 0·02.

Of the six ratios obtained above, one appeared to be completely independent of specimen size; this was l./b. carapace. Means ($\overline{X}$) and standard deviations (s) were obtained and data for '*P. gladiator* Fabr.' are ($\overline{X}$ 0·557, s 0·020, n 55) and for *P. pseudoargentatus* are ($\overline{X}$ 0·565, s 0·050, n 8). Clearly there is no significant difference.

Further analyses showed there was no significant difference between males of '*P. gladiator* Fabr.' ($\overline{X}$ 0·555, s 0·017, n 32) and females ($\overline{X}$ 0·559, s 0·020, n 23).

Other ratios in which there were possibilities of a size factor are given as scatter diagrams. These are l./b. ultimate segment male abdomen (Fig. 1), l./max.b. penultimate segment (Fig. 2), and l. ultimate/ l. penultimate segment (Fig. 3). The first of these shows that the two 'species' overlap extensively in their ratios, with one specimen (29 mm) of *P. pseudoargentatus* lower than and separated from the remainder. The second is similar, with in this case a different specimen of *P. pseudoargentatus* higher than and separated from the remainder. The third again shows overlap, with the 29 mm specimen and the 35 mm holotype of *P. pseudoargentatus* lower than the remainder. Clearly if all specimens labelled as *P. pseudoargentatus* have been correctly identified, this species cannot be separated from '*P. gladiator* Fabr.' It should be noted that the holotype of *P. pseudoargentatus* is at the extreme of the range as regards the ratio l. ultimate/l. penultimate segment of male abdomen.

The two remaining ratios show clear indications of dependence upon specimen size (see Figs. 4 and 5). Easy conversions of data (e.g. logarithmic) failed to produce straight line regressions, so data are considered on the bases of the scatter diagrams.

FIG. 1: Length/breadth of ultimate segment of male abdomen against carapace length in mm. Each symbol represents one specimen with ● originally identified as *P. gladiator* Fabricius; ■ originally identified as *P. pseudoargentatus* Stephenson; and ✱ juvenile specimen.

FIG. 2: Length/maximum breadth of penultimate segment of male abdomen against carapace length in mm. Symbols as in Fig. 1, each symbol represents one specimen.

FIG. 3: Length of ultimate segment of male abdomen/length of penultimate segment against carapace length in mm. Symbols as in Fig. 1, each symbol represents one specimen.

FIG. 4: Maximum breadth minus minimum breadth/minimum breadth of penultimate segment of male abdomen against carapace length in mm. Symbols as in Fig. 1, each symbol representing one specimen.

FIG. 5: Length/breadth of merus of fifth leg against carapace length in mm. Symbols as in Fig. 1, each symbol represents one merus, in most cases two per specimen.

FIG 1

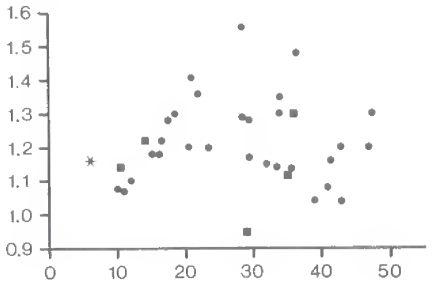

FIG 2

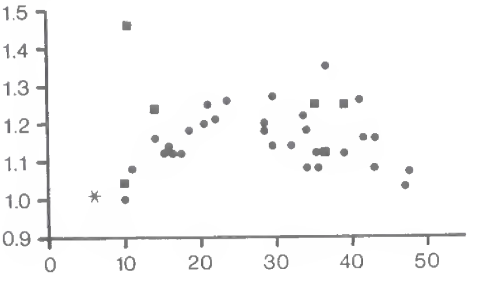

FIG 3

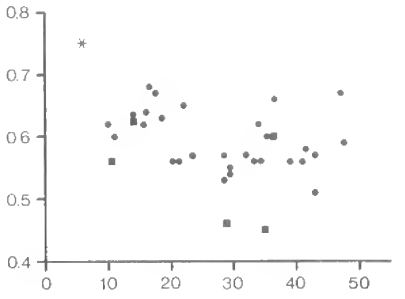

FIG 4

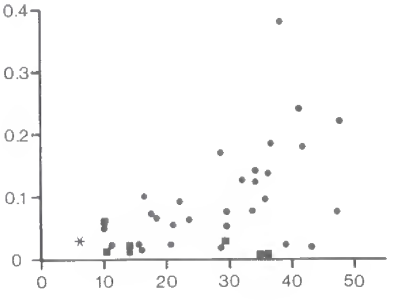

FIG 5

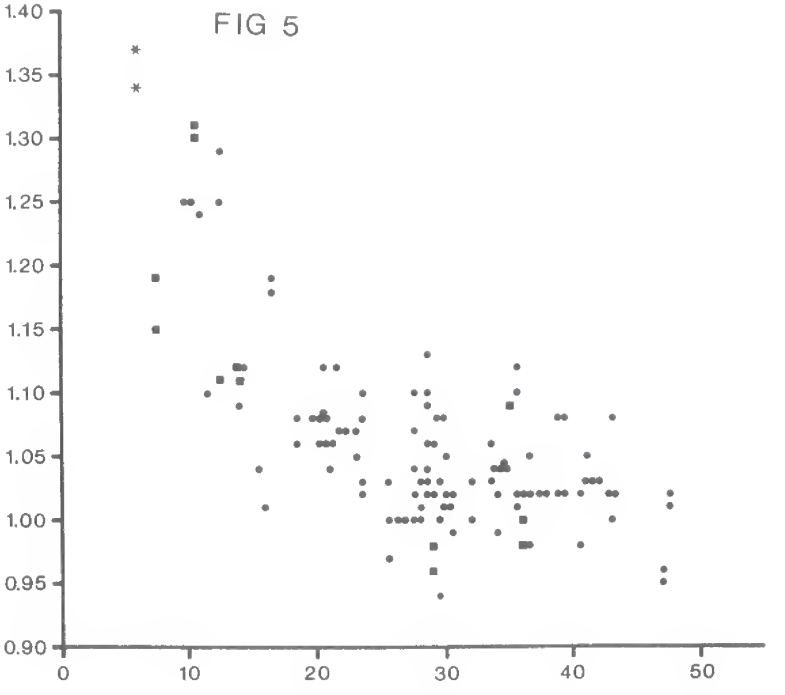

Figure 5 shows that the l./b. ratio of the fifth merus decreases with increasing size of specimen. The 35 mm holotype of *P. pseudoargentatus* lies within the range shown by '*P. gladiator*' material. A 6 mm specimen which we had considered to belong to *P. pseudoargentatus* partly on the basis of a high ratio, apparently owes this to its small size. Figure 4 indicates the concavity of the penultimate segment of the male abdomen in terms of the ratio max. b. — min. b./min. b. All six specimens identified as *P. pseudoargentatus* give low ratios, and once again the holotype has the most extreme value. Because of overlap in values, concavity of this segment would not appear to have diagnostic value.

In summary, biometric study appears to show a complete gradation between specimens identified as *P. gladiator* Fabr. and *P. pseudoargentatus* respectively. In three of the six data sets, the holotype of *P. pseudoargentatus* is at or close to the extreme of the extensive ranges.

(B) Male First Pleopods (Figs. 6A–I, 8A–I, 9A–I)

Only a few species of the genus *Portunus* have pleopods sufficiently unique to give easy diagnosis—examples are *P. granulatus* (H. Milne Edwards) and *P. dubius* (Laurie). In the remainder the general shape and the nature of the subterminal armature are of value, but require detailed descriptions and figures. In some cases pleopod structure varies within a species and in *P. argentatus* (A. Milne Edwards), Stephenson and Rees (1967a) showed that there were two 'forms' differing only in male first pleopods and abdomens. In *P. rugosus* (A. Milne Edwards) the above authors again showed that two 'forms' existed, separated by the male first pleopods and other structures. Variation in pleopod structure in further species of *Portunus* is less well documentated, but Stephenson (1968) has noted that this does occur in specimens of *P. pelagicus* from widely separated areas. With this knowledge of the potential variability of male first pleopods in certain *Portunus* spp., their structures in the present complex were investigated in detail in the available specimens of '*P. gladiator* Fabr.' and *P. pseudoargentatus*.

Figures and descriptions of the pleopods of *P. gladiator* Fabricius and *P. pseudoargentatus* Stephenson are given by Crosnier (1962, figs. 82–3, p. 52) and by Stephenson (1961, figs. 2A, 3F, p. 110) respectively, and Crosnier (p. 148) gives additional comments. The following features have been used for separation:

(1) greater curvature near the middle of *P. pseudoargentatus*. Crosnier (p. 52) states of *P. gladiator* '. . . . recourbé à angle droit vers son milieu . . . .', and of *P. pseudoargentatus* '. . . plus recourbé en son milieu . . .'. Actually Crosnier's figure of *P. gladiator* (fig. 78) shows an angle a little greater than 90°, and not sensibly different from Stephenson's figure of *P. pseudoargentatus* (fig. 2A).

(2) broader tip in *P. pseudoargentatus* (fide Crosnier). This is apparent in the figures quoted above.

In addition Stephenson's figures of the armature of the top of the pleopod in *P. pseudoargentatus* (Fig. 3F) shows a much denser pattern of spinules than Crosnier shows in *P. gladiator* (figs. 82–3).

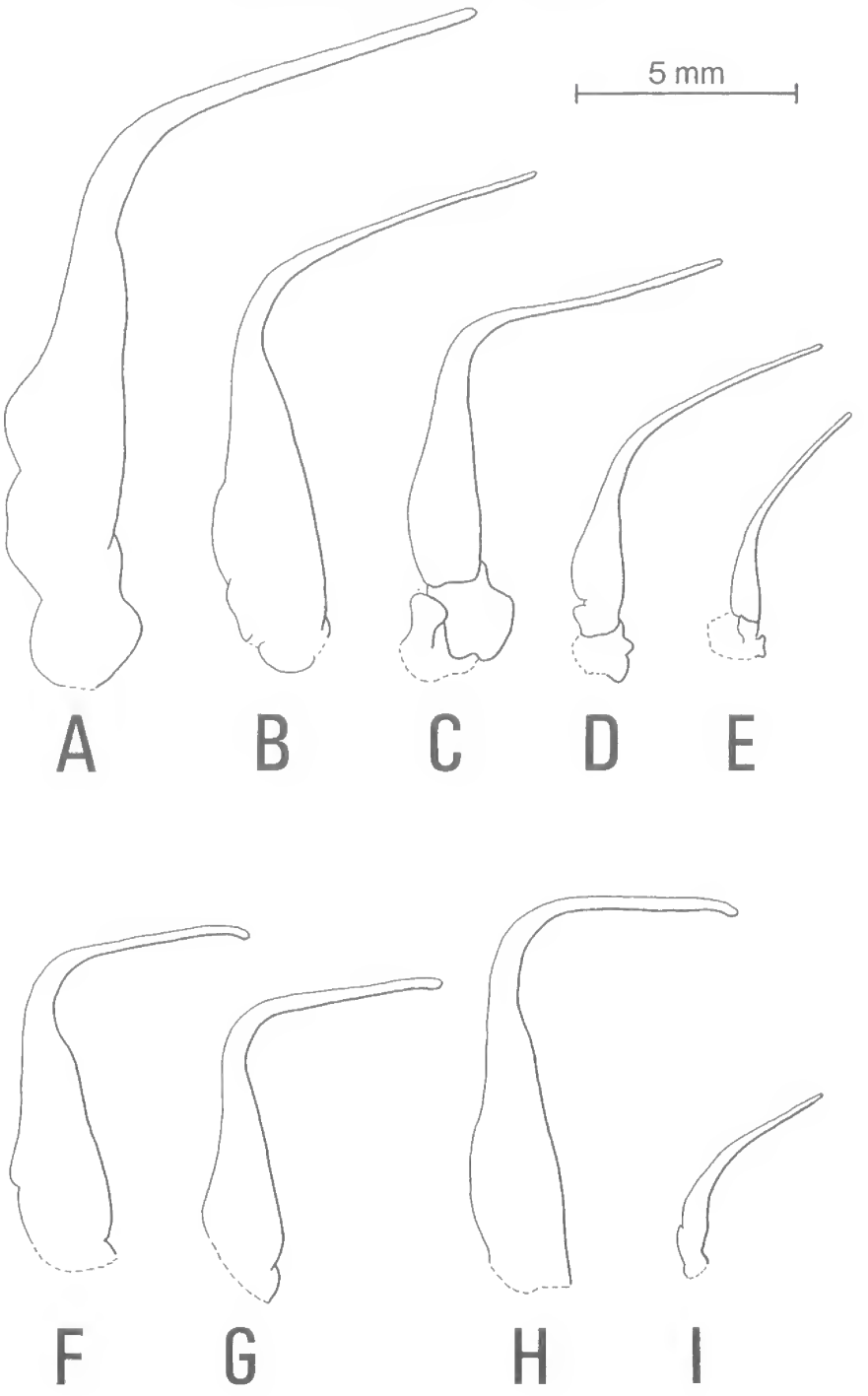

FIG. 6: Male first pleopods. A–E, *P. haanii* showing 'normal' increase in curvature with increase in carapace breadth; F–H, *P. haanii* 'unusual' specimens. I, *P. australiensis* holotype. (Details of specimens are preceded with bold capitals in Appendix 1.)

Pleopods of the present specimens (where examinable) mostly belonged to a graded series, related to the size of the specimens. The general form of the pleopod in members of this series is shown in Figs. 6A–E. Three specimens did not exactly agree with this series. Compared with pleopods of the same general size they had greater curvature near their centres, and had stouter tips. These are shown in Figs. 6F, G, H; F and G being from the (only) two specimens in one collection. H is from the holotype of *P. pseudo-argentatus*.

The two diagnostic features of *P. pseudoargentatus* are confirmed for the holotype, but are equally exhibited by two specimens which in all other particulars appear to be typical *P. gladiator* Fabricius.

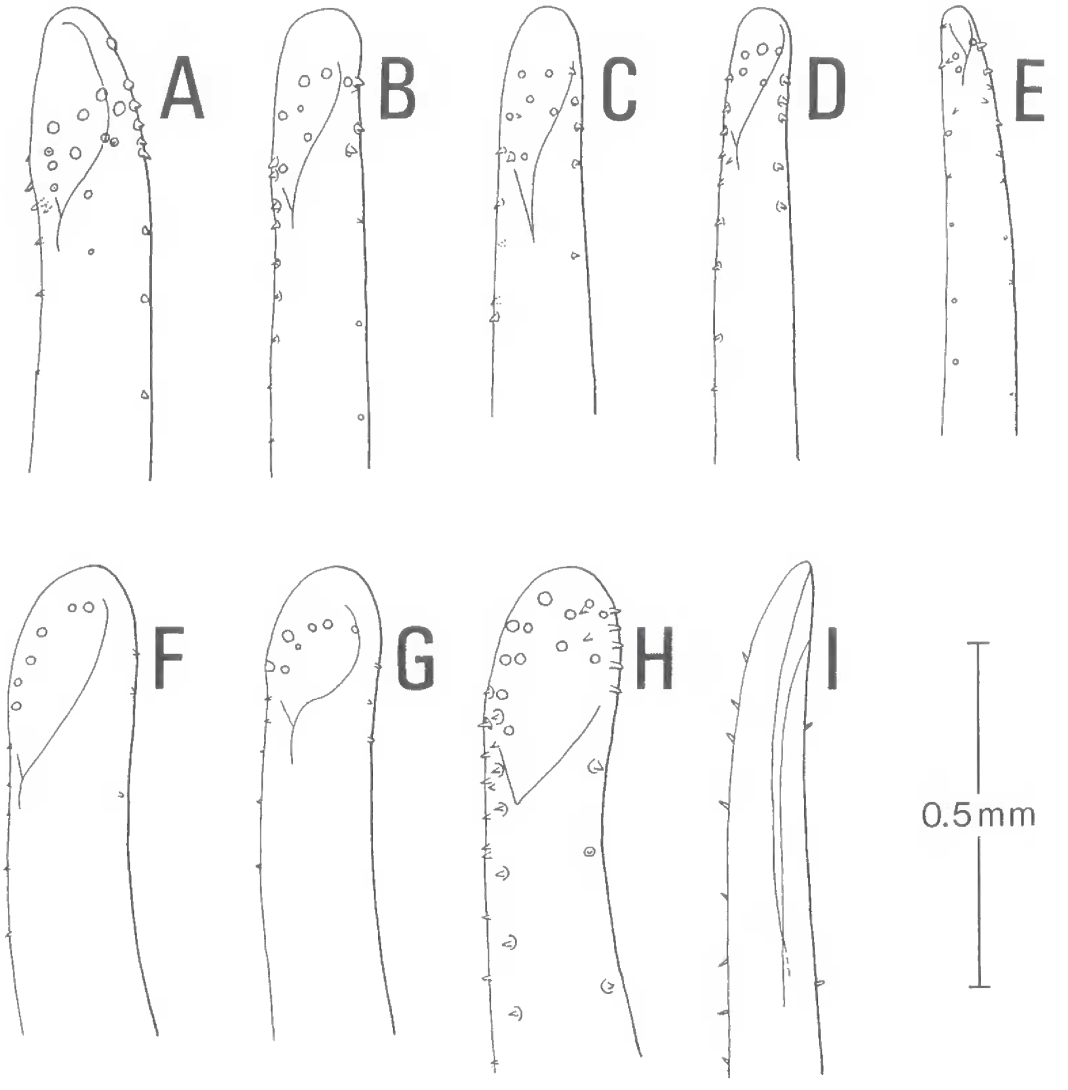

FIG. 7: Upper surface of tips of male first pleopods. Specimens as in Fig. 6.

Tips of pleopods of the above specimens are shown in Figs. 7A–H, 8A–H. These confirm the relative robustness of the tips of specimens F, G and H and show considerable variation in the subterminal armature. Difficulties were encountered in elucidating the details of this spinulation, particularly in the thin terminal area beyond the aperture of the appendage. Here each spinule arises from a roughly circular area, more transparent than its surroundings, and these areas are more clearly visible in a ventral view of the appendage. However, in those cases where spinules could be recognised these are directed dorsally.

Common features in all pleopods were relative absence of spinules from upper and under surfaces (excepting in their terminal area), lines of spinules on or near both inner and outer sides, and a band of spinules near the tip directed into the flaring portion of the aperture.

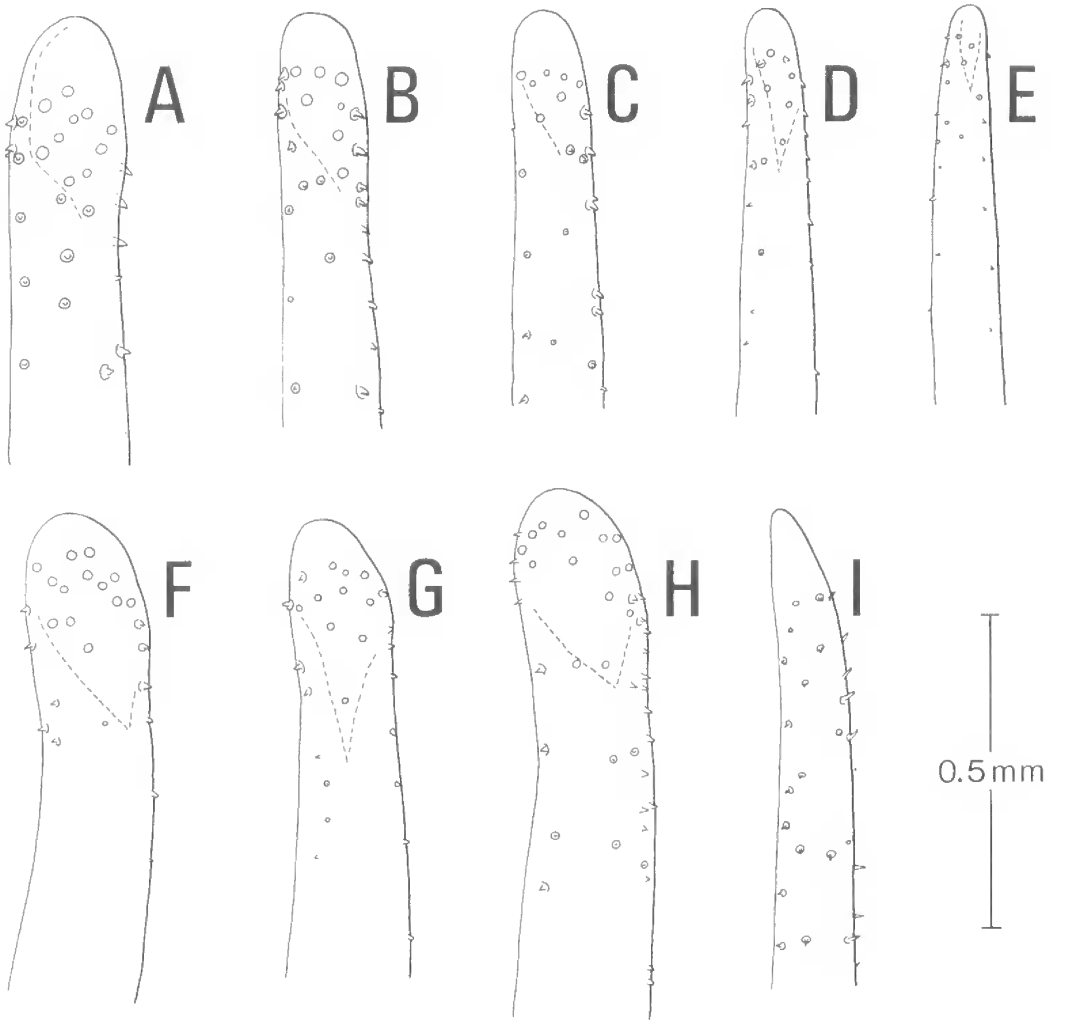

FIG. 8: Lower surface of tips of male first pleopods. Specimens as in Fig. 6.

In the series A–E with increasing size of appendage, the spinules become larger and more numerous, with subterminal concentrations on inner and outer sides. In F and G the spinules are relatively small for the size of the appendage, are sparsely distributed on inner and outer sides, and are without the subterminal concentrations. In H the spinules are smaller but are more numerous than from appendages of the same size in the A–E series. The upper surface bears a row of spinules near its outer margin which is not or is scarcely recognisable on the remainder. Figs. 7F, 8F, 7G, 8G, 7H and 8H show a further difference from the remainder of those figures in having the spinules of the thin terminal area extending closer to the tip. This distinction was not absolute; two other specimens otherwise resembling 8B, 9B showed this feature.

Overall it is concluded that all pleopods examined are variants of a single specific pattern. This conclusion has already been indicated in two papers recently published (Stephenson, 1972a, b).

(c) Carapace Granulation and Pigmentation (Figs. 9A, B)

Stephenson and Rees (1967a, p. 25) stated that *P. pseudoargentatus* differs from Crosnier's specimens of *P. gladiator* Fabr. in having: 'A more strongly embossed carapace with coarser granulation. In particular the cardiac, lateral postcardiacs, posterolaterals,

Fig. 9: Carapace granulation. A, *P. haanii* male, Fort-Dauphin,Côte sud de Madagascar, coll. A. Crosnier ex. P.M.; B, *P. haanii* male, Shimizu, Suruga, Japan, U.S.N.M. 112423; C, *P. australiensis*, holotype, A.M. P12602.

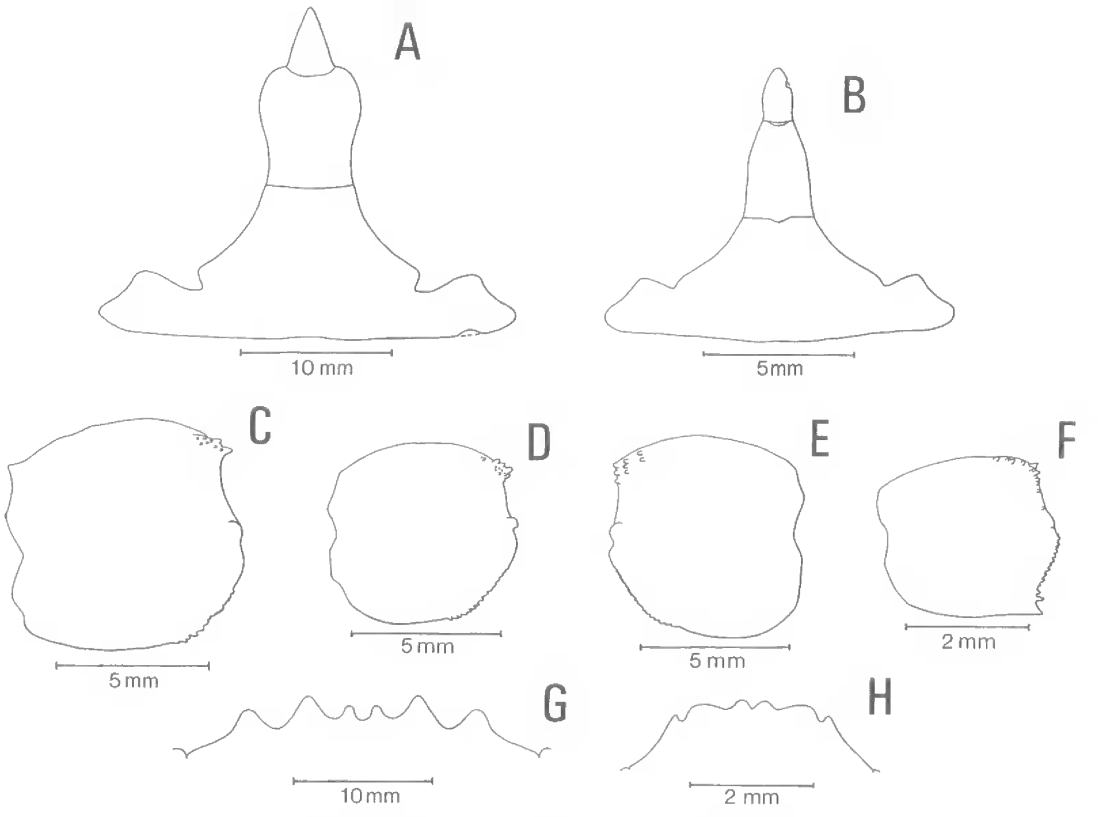

FIG. 10: A, Typical male abdomen *P. haanii* (A.M. W2688); B, Male abdomen *P. australiensis* (A.M. P12602); C, Right merus *P. haanii* (Q.M. W2688); D, Right merus *P. haanii* (U.S.N.M. 72540–54 mm specimen); E, Left merus *P. haanii* (Galathea sta. 346); F, Right merus *P. australiensis* (A.M. P12602); G, Typical carapace front *P. haanii* (Q.M. W2688); H, Front of juvenile *P. haanii* (U.S.N.M. 39801).

and two mesobranchials are larger and less diffuse than in *P. gladiator*.' Examination of the present material showed that there was gradation between strongly embossed carapaces with coarser granulation (which tended to occur in smaller specimens) and less strongly embossed more finely granular carapaces. Figs. 9A, B show the extremes of variation and approximately the average conditions. The variation is expressed verbally in the specific description.

Pigmentation of the holotype of *P. pseudoargentatus,* after two months in alcohol was described by Stephenson (1961). This differs from that of the pigmented specimens of *P. gladiator* Fabricius (as described below) only in the presence of a conspicuous purplish red mark on the propodus of the fifth leg—only the left leg was present. After almost 12 years of alcohol preservation this mark is the only remaining pigmentation and is now pink and presumably on prolonged preservation it will disappear. Apart from the holotype, none of the specimens identified as *P. pseudoargentatus* had any significant pigmentation after preservation.

(D) CONCLUSION

When all specimens previously identified as *P. pseudoargentatus* are compared with those of '*P. gladiator* Fabr.' there is considerable overlap. This is due to the great variability of features which had been used in diagnosis. In a few features the holotype of *P. pseudoargentatus* is at the extreme of a range of variation and while there is not a sufficient gap between this specimen and the remainder to merit retention of specific status, there is a parallel between its morphological status and biogeographic isolation—it is the only existent specimen from Australian waters. If further Australian specimens are obtained and agree closely with the holotype of *P. pseudoargentatus* the possibilities of clines or subspecies of *P. haanii* Stimpson (= *P. gladiator* Fabricius, 1798) will merit investigation.

SYNONYMY OF *P. HAANII*

Portunus gladiator Fabricius, 1798, p. 368. Latreille, 1825, p. 189. Rathbun, 1902, p. 26. Crosnier, 1962, pp. 51–5, 148, 150, figs. 72, 76, 78, 82–3, pl. 3, fig. 2. Sakai, 1965, p. 118, col. pl. 57, fig. 1 (record only). Stephenson and Rees, 1967, pp. 24–5; 1968, p. 293. Stephenson, 1972a, pp. 16, 39; 1972b, p. 135 (record only).

Portunus (*Amphitrite*) *gladiator* Fabricius: de Haan, 1850, p. 39, pl. 1, fig. 5.

Amphitrite Haanii Stimpson, 1858, pp. 38–9; 1907, p. 79.

Neptunus gladiator Fabricius: A. Milne-Edwards, 1861, p. 330. Richters, 1880, p. 152 (record only). Müller, 1886, p. 475 (record only). de Man, 1887, pp. 69–70. Henderson, 1893, p. 367 (record only). Sakai, 1934, p. 303 (record only).

Neptunus (*Amphitrite*) *gladiator* Fabricius: Miers, 1886, p. 177. Ortmann, 1893, p. 73. Alcock, 1899, pp. 35–6. Laurie, 1906, p. 412. Parisi, 1916, p. 173 (record only). Balss, 1922, p. 107. Shen, 1937, pp. 101–3, fig. 2. Sakai, 1939, pp. 390–1, fig. 5, col. pl. 47, fig. 3.

Portunus (*Achelous*) *gladiator* Fabricius: Rathbun, 1910, p. 36 (record only).

Callinectes gladiator Fabricius: Stebbing, 1915, p. 58 (record only).

Monomia gladiator Fabricius: Barnard, 1950, p. 156. Fourmanoir, 1954, p. 9 (record only).

Portunus pseudoargentatus Stephenson, 1961, pp. 109–11, figs. 2A, 3F, pl. 2, fig. 4, pls. 4F, 5D; 1972a, pp. 16, 41–2; 1972b, p. 137. Crosnier, 1962, pp. 148, 150 (under *P. gladiator*). Stephenson and Rees, 1967, p. 25; 1968, pp. 294–5.

[Not] *Cancer gladiator* Fabricius, 1793, p. 449 (= juv. *P. sanguinolentus* (Herbst), fide Latreille, 1825, p. 190).

[Not] *Cancer Menestho* Herbst, 1803, p. 34, pl. 55, fig. 3.

[Not] *Lupea gladiator*: H. Milne Edwards, 1834, p. 456.

[Not] *Portunus* (*Amphitrite*) *gladiator*: de Haan, 1850, p. 65 pl. 18, fig. 1 (= *P. orbitosinus* Rathbun, 1911).

[Not] *Amphitrite media* Stimpson 1858, p. 39; 1907, pp. 79–80, pl. 10, fig. 1 (= ?*P. orbitosinus* Rathbun, 1911).

[Not] *Callinectes tumidus* Ordway var. *gladiator* Benedict, 1893, p. 537, fide Barnard, 1950, p. 156.

[Not] *Portunus gladiator*: Stephenson and Campbell, 1959, pp. 110–1, figs. 2J, 3J, pl. 3, fig. 2, pls. 4I, 5J (not 4J as stated) (= *P. australiensis* sp. nov. (see later)).

[?] *Amphitrite gladiator* (Fabricius): Haswell, 1882, p. 84.

As indicated in the introduction the first use of the epithet *gladiator* is in Fabricius (1793, p. 449) with reference to *Cancer gladiator*, which Latreille (1825, p. 190) in company with Fabricius's *C. defensor,* lists as a synonym of *P. sanguinolentus* (Herbst).

Fabricius's above description of *C. gladiator* is so generalised that it could apply to many species. It almost certainly does not apply to the species he called *Portunus gladiator* in 1798 (p. 368) (and which has become accepted as *the P. gladiator*). Further evidence is that the habitat of *C. gladiator* is stated as 'in Nova Hollandia Mus. Dom. Banks'. As indicated, *P. gladiator* appears to occur quite rarely in Nova Hollandia (= Australia). It is clear that whether or not we accept Latreille's synonymisation of *Cancer gladiator* Fabricius; 1793, under *P. sanguinolentus* (Herbst, 1783):

(a) *C. gladiator* Fabricius, 1793, is in the same genus as his *P. gladiator*;
(b) the two are different species;
(c) following the first use of the epithet *gladiator* the second use is as a junior homonym; and
(d) hence under the International Rules the name should be replaced.

The next possible name is *Cancer menestho* Herbst, 1803, which Latreille (p. 189) gives as a queried synonym of Fabricius's *P. gladiator*. Later workers have omitted the query without justifying so doing. Herbst's figure (fig. 3) shows a *Portunus* with the posterior border of the arms of the chelipeds showing one distinct and protruding spine and a second non-protruding spine. Herbst's text states (pp. 35–6): 'Am innern Rande des Armes steht eine Reihe von vier nach vorne sich hinneigender Dornen, die nach oben zu werden etwas grösser; am Aussenrande steht ganz oben ein gleicher Dorn; bey grossen Exemplaren steht etwas hinter diesem noch ein zweiter von gleicher Grösse, bey den kleiner ist dasebst nur eine stumpfe Ecke. . . .'. All the present specimens including the smallest of *P. haanii* have two distinct spines on the posterior border of the arm, and on this basis Herbst's species is not a synonym. It might be *P. rubromarginatus* (Lanchester) but this has only a single spine on the posterior border of the arm and has a characteristic pigmentation which differs from that of *Cancer menestho*. Unless and until the range of Herbst's specimens can be re-examined their status must remain uncertain.

The first available specific epithet is *haanii*, used by Stimpson (1858, p. 38), but meanwhile in the chronology of the synonymy Latreille (1825, p. 189) is interesting. Referring to segments of the (male) abdomen he states: '. . . . l'avant-dernier un peu dilaté et arrondi latéralement à son extrémité.' He clearly refers to a '*P. pseudoargentatus*' form of abdomen.

H. Milne Edwards's (1834, p. 456) description of *Lupea gladiator* has been accepted into the synonymy by all later workers with the exception of Stimpson (1858, p. 38; 1907 p. 79) who noted that H. Milne Edwards's description of the carapace as 'peu ou point granuleuse' did not apply to de Haan's *Portunus* (*Amphitrite*) *gladiator* (see below). Stimpson evidently accepted that Milne Edwards's *L. gladiator* was Fabricius's *P. gladiator* and proposed the new name *Amphitrite Haanii* for de Haan's form. In fact de Haan's species is the same as Fabricius's (but see below), and the 'different' species, whose synonymy is uncertain appears to be Milne Edwards's. Further evidence for this is that Milne Edwards describes the front as 'très-relevé' which it is not.

De Haan (1850) gave a good figure of the present species (pl. 1, fig. 5) but a second figure (pl. 18, fig. 1) supposedly of this species is *P. orbitosinus* Rathbun.

Stimpson (1858) introduced two names, *Amphitrite Haanii* (p. 38) already commented on, and *A. media* (p. 39). The latter, which has not been figured, differs from the former in

having a shorter last anterolateral tooth, and the lateral and median frontal teeth of similar size. A. Milne Edwards (1861, p. 331) under *Neptunus medius* thought it was insufficiently precise to distinguish it from *P. gladiator* Fabricius, and this opinion was repeated by Ortmann (1893, p. 73). Alcock (1899, p. 35) accepted *A. media* as a queried synonym of *P. gladiator* Fabricius but it seems clear that it is not a synonym because of the noticeable difference in frontal teeth. Rathbun (1910) accepted this, but not Parisi (1916). It is unfortunate that Stimpson's type is not extant, because *A. media* greatly resembles *P. orbitosinus* Rathbun, and if they are identical, the former name would have priority.

Much of the synonymy is concerned with generic and subgeneric names, whose history need not be detailed; it has been outlined by Rathbun (1930, p. 33). A decision by the International Commission on Zoological Nomenclature (1956) has established the generic name as *Portunus,* and Stephenson and Campbell (1959) and Stephenson, Williams and Lance (1968) have concluded that there are no acceptable sub-generic divisions.

The most recent synonymy confusion owes much to the present senior author. The specimens which Stephenson and Campbell (1959) referred to *P. gladiator* belong to a different species, while, as shown earlier *P. pseudoargentatus* belongs to the present species.

DESCRIPTIONS OF SPECIES

P. haanii Stimpson (= *P. gladiator* Fabricius, 1798) is redescribed taking cognisance of its variablity, and to include *P. pseudoargentatus*. The material identified as *P. gladiator* Fabricius by Stephenson and Campbell (1959) is renamed *P. australiensis* sp. nov. and also redescribed to clarify and amplify its distinctiveness from *P. haanii*. To avoid repetition, features common to the two species are listed first and not repeated. The species (with synonymy of one) are then described, with the full lists of specimens examined being listed in Appendix 1.

Features Common to Both Species

Front: Four-lobed, laterals at least width of medians. Lower border of orbit with distinct tooth close to basal antennal joint.

Anterolateral Teeth: First stout and blunt, ninth a long spine directed outwards, second to eighth of progressively increasing length.

Carapace: Moderately broad (breadth ca. 1·8 times length). Anterolateral borders forming broad curve whose centre lies at or behind cardiac region. Postlateral junctions rounded and with right-angled projection on lower plane. Surface covered with widely spaced granulated areas separated by regions of dense pubescence. Granulated patches are: protogastrics, diffuse; mesogastrics; central gastric; metagastrics with distinct anterior termination; 2 cardiacs and 3 postcardiacs; anterolaterals; epibranchial; either 3 or 4 mesobranchials; 2 lateral postcardiacs and postlaterals; metagastrics forming broad transverse band with distinct almost ridge-like anterior termination.

CHELIPEDS: Stout, pubescent. Posterodistal border of arm bearing 2 sharp spines, anterior border with 4 spines. Wrist with 2 usual spines. Three usual carinae on upper surface of hand of which only innermost ends in a spine. Outer surface of hand with very distinct carina. Under surface of hand of cheliped typically bearing squamiform granules.

THIRD MAXILLIPED: Anteroexternal angle of merus strongly produced in lateral direction.

FIFTH LEG: Merus relatively long; 1/b = 0·96–1·10.

Portunus haanii (Stimpson, 1858)

(Figs. 6A–H, 7A–H, 8A–H, 9A–B, 10A, C–E, G–H)

DESCRIPTION

FRONT: Laterals rounded, or acute or right-angled, ca. three times width of medians, these usually rounded, sometimes acute. Upper border or orbit with distinct and prominent tooth (less distinct in small specimens). In smaller specimens indentation of front becomes shallower so that teeth appear relatively broader and front as a whole becomes increasingly sinuous.

ANTEROLATERAL TEETH: Second to eighth sharp although rounded in larger or worn specimens.

CARAPACE: In large specimens granulated area a relatively small proportion of total carapace area, in smaller specimens a relatively greater proportion granulated but still distinctly less than in *P. australiensis*. Frontal granular patches present; orbitals inconspicuous or absent. Postfrontals either absent or represented by patch of 2 to 8 granules. Protogastrics forming broad diffuse arc. Central gastric broad and diffuse with about 3 to 4 irregular rows of granules. Each mesogastric consisting of two widely separated ovoid patches. Two cardiacs well separated. Median postcardiacs small. Lateral postcardiacs relatively small. Anterolaterals consisting of relatively narrow and diffuse patches opposite second to fourth and fifth to sixth teeth, sometimes a few granules on bases of seventh and eighth teeth. Epibranchials almost forming curved ridges bearing a few scattered granules anterior to them. Four distinct and well separated mesobranchials. Postlaterals small and distinct

CHELIPEDS: Inner carina of upper surface of palm with relatively large subterminal spine. Outer surface of palm beneath pile of hairs not or faintly squamiform. In large males on inner surface of palm of cheliped a conspicuously granular central carina, with scattered granules lying on either side of it. In smaller males and in females central carina ill-developed and tending to squamiform. Inner sides of fingers strongly carinate and in large males, granular.

FIFTH LEG: Merus with anterodistal extremity typically with conspicuous projection consisting of numerous rounded or spiniform granules. In some relatively small specimens projection not conspicuous and merely a coarsely granular area. Posterodistal

border with regularly arranged granules (rounded or sharp) giving serrated appearance but without conspicuous projection.

MALE ABDOMEN: Somewhat variable in shape with penultimate segment in larger specimens distinctly swollen in distal third but not swollen in smaller specimens. Ultimate segment in larger specimens with concave lateral borders, in smaller specimens with convex borders. Ultimate segment ca. half length of penultimate (0·44–0·61 times). Ultimate segment slightly longer than broad (1·07–1·36 times). Penultimate segment also slightly longer than broad (1·06–1·43 times).

COLOUR: After prolonged alcohol preservation patches of pink pigment on proximal ends of spines of anterior border of arm, bases of inner wrist spines, two patches on inner carina on upper surface of palm, mottled patching on upper and outer surfaces of movable finger, also in groove between outer frontal tooth and inner supraorbital border and between inner and outer frontal teeth. In specimens kept for shorter period in alcohol e.g. seven years, additional areas of pink pigmentation are: posterior margin of carapace, postlateral granules, patches on upper surface of hand of cheliped and in one case on most carapace granules.

Portunus australiensis sp. nov.

(Figs. 6I, 7I, 8I, 9C, 10B, F.)

Portunus gladiator: Stephenson and Campbell, 1959, pp. 110–1, figs. 2J, 3J, pl. 3, fig. 2, pls. 4I, 5J (not 4J as stated). Stephenson and Rees, 1967a, p. 24.

[Not] *Portunus gladiator* Fabricius, 1798, p. 368.

MATERIAL EXAMINED

HOLOTYPE: ♂ (28 mm), Ninety-Mile Beach between Cape Jaubert and Wallal, dredged 5 fm, Sept. 1929, A.M. P12602.

ALLOTYPE: ♀ (44 mm), dredged between C. Bossut and Broome, 5 fm, 11.x.1929, A.M. P12596.

DESCRIPTION

FRONT: Laterals ca. right-angled, about twice width of medians which are acute or rounded. Upper border of orbit without distinct and prominent tooth.

ANTEROLATERAL TEETH: Second to fourth blunt or right-angled, fifth to eighth sharp.

CARAPACE: Frontals and orbitals obvious in male but not in female specimen. Postfrontals represented by line of 3 or 4 granules. Protogastrics almost subdivided into 2, posterior portion merging with mesogastrics almost to form a granulated ridge. Central gastric narrow, anterior to mesogastric about 2 irregular rows of granules, posteriorly a single row. Mesogastrics forming transverse band with distinct anterior termination. Two cardiacs almost confluent. Median postcardiacs broad diffuse patch running almost to posterior border of carapace. Lateral postcardiacs relatively large. Anterolaterals consisting of relatively broad and dense patches of granules opposite second to fourth,

fifth to sixth and seventh to eighth teeth. Epibranchials forming almost straight ridges of granules with numerous scattered granules anterior to them. Two distinct anterior mesobranchials, posterior mesobranchial granulated areas merging into posterior laterals.

CHELIPEDS: Inner carina of upper surface of palm with relatively small terminal spine. Outer surface of palm with distinctly squamiform granules. Inner surface of palm of cheliped with central carina, of squamiform granules, with squamiform areas lying above it. Inner sides of fingers weakly carinate and not obviously granular.

FIFTH LEG: Merus with anterodistal extremity with inconspicuous cluster of spiniform granules. Posterodistal border serrated and with one or two distinct spines marking the edge of the border.

MALE ABDOMEN: Penultimate segment markedly converging in distal third, ultimate segment with convex lateral borders. Penultimate segment longer than broad (1·20 times). Ultimate segment much longer than broad (1·35 times), ca. half length of penultimate (0·56 times).

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APPENDIX 1

MATERIAL EXAMINED OF *P. haanii* STIMPSON.

Illustrated specimens indicated by bold capitals.

Australian Museum: One ♀ (47 mm), P7680. One ♂ (62 mm), P7681, Ceylon, Pearl Banks Inspection, Moderagam Paar, 26.xi.1921; exchange Colombo Museum, Ceylon, Jan. 1925. One ♀ (44 mm), P14193, Troubadour Reef, approx. 10°S. 129°E., edge of Sahul Shelf, off Darwin, N.T., caught with dip net at surface over 17 fms 20.30 hrs, 6.ix.1949, coll. G. P. Whitley, 'Stanley Fowler' C.S.I.R.O. Exped.

British Museum: Four ♀ (37–57 mm), BM315–318, Madras, 15.vii.1892, coll. Henderson. One ♂ (74 mm), BM289, off Negambo, Gulf of Manaar, Ceylon, 22.v.1907, coll. Herdman. **E** One ♂ (28 mm), BM118, off Kaltura, 16.i.1934, coll. Herdman. Three ♂ (25–39 mm); one ♀ ovig (37 mm), BM116–117, Ceylon, Pearl Banks, Gulf of Manaar, 16.i.1934, coll. Herdman.

Office de la Recherche Scientifique et Technique Outre-Mer, Madagascar: One ♂ (84 mm), Fort-Dauphin, Côte sud de Madagascar, dans une nasse à langoustes, 20 m, coll. A. Crosnier. One ♀ (71 mm), Cap St André, Côte nord-ouest de Madagascar, chalutage 20 m sable vasard., Juillet 1959, coll. A. Crosnier.

Paris Museum: One ♂ (52·5 mm), det. Crosnier 1962 *P. pseudoargentatus* Stephenson. One ♂ (66·5 mm), Sumatra, coll. M. Martin. **A** One ♂ (82 mm), Fort-Dauphin, Côte sud Madagascar, dans nasse à langoustes, Mai 1961, 20 m, coll. A. Crosnier.

Queensland Museum: **B** One ♂ (66 mm), W2688, NW Madagascar (from Dr A. Crosnier).

Strasbourg Museum: One ♂ (27 mm), dry, Kagoshima, Japan, 1882, coll. L. Döderlein. One ♂ (64·5 mm), Kochi, Japan, 1882, coll. L. Döderlein. (Previously identified as *P. pseudoargentatus* Stephenson, see Crosnier, 1962). Two ♂ (52 mm, other damaged); one ♀ (62 mm), Kochi, Japan, 1882, coll. L. Döderlein.

United States National Museum: One ♂ (70 mm); one ♀ (66 mm), dry, U.S.N.M. 112354, Natal, prob. S. Africa, from W. F. H. Rosenberg. (See Stephenson and Rees 1967a). Two ♂ (**G**54 **F**55·5 mm), U.S.N.M. 72540, Yenosima, mouth of Bay of Jeddo, Japan, coll. E. S. Morse, 594 Boston Soc. Nat. Hist. One ♀ ovig (39 mm), U.S.N.M. 72533, Yenosima, mouth of Bay of Jeddo, Japan, coll. E. S. Morse, 595 Boston Soc. Nat. Hist. One ♀ (35 mm), U.S.N.M. 45882, Wakanoura, Kishu, Japan, exchanged Imper. Univ. Tokyo. One ♂ (77 mm); one ♀ (53 mm), U.S.N.M. 26254, Nakanoura, Kü, Japan, Jordan and Snyder, 1900, Stanford Univ. One juv. (6 mm), U.S.N.M. 39801, between Koh Riat and Koh Mesan, Gulf of Siam 7.ii.1900, 3–5 fms, coll. Th. Mortensen. One ♂ (19·5 mm), U.S.N.M. 112423, Shimizu, Suruga, Japan, 'Albatross', 14.x.1906, shore. (Previously identified as *P. pseudoargentatus* Stephenson; see Stephenson and Rees 1967a). One ♀ (35 mm), U.S.N.M. 54519, Yamagata Prefecture, Japan, August 1917, coll. M. Sasaki, badly damaged. One ♂ (37 mm), U.S.N.M. 60250, Toyama Bay, Honshu, Japan, from Hakkaido Imperial University, coll. M. Sasaki 1925. One ♂ (25 mm), U.S.N.M. 112434, Lembeh Strait, Celebes, Philippines, 14.vi.1929, coll. Herre. (Previously identified as *P. pseudoargentatus* Stephenson; see Stephenson and Rees, 1967a). Two ♀ (51 mm), U.S.N.M. 127068, Indian Ocean, 9° 13′N., 95° 51′E., 23.iii.1963, 60–50 fms, Anton Bruun sta. AB-20 cruise 1, Indian Ocean Exped. 'Anton Bruun', 31.vii.1963. One ♂ (32 mm), U.S.N.M. 127069, Indian Ocean, 17° 41′N., 71° 33′E., to 17° 45′N., 71° 32′E., 14.xi.1963, 90 fms, Anton Bruun. (This specimen has a distinctly swollen branchial region but no trace of parasites is evident.)

Universitets Zoologiske Museum, Copenhagen: One ♂ (72 mm), dry, Tranquebar, Daldot (Fabricius, 1798 type). Two specimens (45 and 54 mm), photographs only, Tranquebar, Daldot (Fabricius original). One ♀ (ca 19 mm), Singapore, 4.vi.1903, low water. One ♂ (18 mm), off Jola, Philippines, 19.iii.1914, ca. 25 fms, sand, coll. Th. Mortensen. (Previously identified as *P. pseudoargentatus* Stephenson; see Stephenson, 1972a). One ♀ (24·5 mm), Misaki, 26.iv.1914, ca. 3 fms, coll. Th. Mortensen. (Previously identified as *P. gladiator* Stephenson and Campbell; see Stephenson, 1972a). One ♂ (18 mm), Misaki, ca. 10 fms, Grus, 30.iv.1914, coll. Th. Mortensen. (Previously identified as *P. gladiator* Stephenson and Campbell; see Stephenson, 1972a). One ♂ (18·5 mm), Misaki, 9.vi.1914, ca. 25 fms, sand, coll. Th. Mortensen. One ♂ (30 mm), Sunda Strait, Dan Kai Is. Exped. sta. 75, 6° 10′S., 105° 44′E., 29.vii.1922, 40 m, sand and shells. One ♂ (18 mm), Java Sea, Dan Kai Is. Exped. sta. 118, 7.viii.1922, 27 m, sand and shell, Sigsbee trawl. (Previously identified as *P. pseudoargentatus* Stephenson; see Stephenson, 1972a). One ♂ (56·5 mm), 1½ miles east of Tanjong Rhu, off Singapore, Galathea sta. 346, 23.v.1951, 14 m, sand and mud, 1530–1600 hrs. Four ♂ (41–80 mm) and two ♀ (51–61 mm), West Malay Peninsula, Thai Dan. Exped. just after sta. 1023, 14.i.1966. **D** One ♂ (36·5 mm) and two ♀ (35–39·5 mm), West Malay Pensula, Thai. Dan. Exped. sta. 1153, 9° 12′N., 98° 15′E., 5.iii.1966, 17 m, fine sand. One ♀ (55 mm), West Malay Peninsula, Thai. Dan. Exped. sta. 1171, 9° 13′N., 97° 50′E., 7.iii.1966, 70 m, mud with

many large shells. One ♂ (61·5 mm), West Malay Peninsula, Thai. Dan. Exped. sta. 1179, 8° 08′N., 98° 17′E., 9.iii.1966, 18 m, sandy mud.

Western Australian Museum: Three ♂ (28–62 mm, **C** = 54 mm); one ♂ with *Sacculina* (ca. 29 mm); one ♀ (37 mm) and one ♀ ovig (47 mm), W. A. M. 111–71, Ceylon with consignment from Mullaitivu Mud Banks, coll. G. H. P. De Bruin. **H** One ♂ (63 mm) W.A.M. 50–60, 5 miles NW. Gun Island W.A., Southern group Abrolhos Is. 11.v.1960, 30–35 fms, coral rubble, sponge and weed, coll. R. W. George on 'Davena'. (Holotype of *P. pseudoargentatus* Stephenson; see Stephenson, 1961). One ♀ with *Sacculina* (47 mm), W.A.M. 101–71, near Siasi Is., Sulu Arch., 17.ii.1964, sand, coll. B. R. Wilson on 'Pele'.

APPENDIX 2

Specimens Previously Identified as *Portunus gladiator* Fabricius.

Portunus argentatus (A. Milne Edwards): One ♀ (18·5 mm), W.A.M. 103–71, NW. of Bluff Pt., Geraldton, W.A., 27° 40′S., 113° 03′E., 36 m, C.S.I.R.O. sta 131, 22.viii.1963. Two ♂ immature (15 mm), W.A.M. 107–71, NW. of Carnarvon, W.A., 24° 00′S., 112° 51′E., 130 m, C.S.I.R.O. sta 29, 2.ii.1964.

Portunus brockii (de Man): Three ♂ (21·5–27 mm) and two ♀ (15–23 mm), U.S.N.M. 73153, Iloilo, Panay Id., Philippines, coll. H. C. Kellers, March–May 1929.

Portunus gracilimanus (Stimpson): One ♀ (18 mm) and one ovig. ♀ (19·5 mm), W.A.M. 110–71, Coronado Bay, Mindanao, Sulu Sea, 46–130 m., sand and mud, coll. M. King on 'Pele', 10.ii.1964. One ♂ (40 mm), W.A.M. 104–71, Gulf of Carpentaria Prawn Survey, sta. 1541, coll. R. W. George on 'Rama', November 1964. One ♂ (27 mm), W.A.M. 106–71, Ceylon, with a consignment from Mullaitivu Mud Banks, coll. G. H. P. de Bruin.

Portunus granulatus (H. Milne Edwards): Five ♂ (15–26 mm) and six ♀ (21·5–30·5 mm), U.S.N.M. 75885, Benkulen, Sumatra, coll. H. C. Kellers, November 1925.

Portunus rubromarginatus (Lanchester): One ♀ (42 mm), W.A.M. 109–71, Shark Bay, W.A., 17 m, coll. E. Barker, 18.x.1964. One ♀ (45 mm), W.A.M. 108–71, Shark Bay, W.A., coll. W. and W. Poole Bros., August 1965. One ovig ♀ (47 mm), W.A.M. 105–71, Shark Bay, W.A., coll. A. McKenzie, August 1965. One ♂ (40 mm) and two ♀ (36·5–38·5 mm), A.M. P.16826, ½ mile S. of western end of One Tree Island reef, Capricorn Group, Great Barrier Reef, Queensland, 50 m, sand and shell, coll. J. Paxton and B. Goldman, 5.ii.1969.